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Responses of soil fauna community under changing environmental conditions

KUDURETI Ayijiamali[1,2], ZHAO Shuai[1*], Dina ZHAKYP[3], TIAN Changyan[1*]

[1] State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China;
[2] University of Chinese Academy of Sciences, Beijing 100049, China;
[3] Saken Seifullin Kazakh Agrotechnical University, Astana 010000, Kazakhstan

Abstract: Soil faunas account for 23% of known animal species and play a crucial role in ecosystem processes such as mineralizing nutrients, regulating microbial community composition, forming soil aggregates, and enhancing primary productivity. However, due to global climate change, population density, community composition, and distribution patterns of soil fauna vary. Understanding the responses of soil fauna to major environmental change facilitate the conservation of biodiversity. Therefore, a review work of recent researches for analysing the effects of key environmental factors on soil fauna, such as warming, drought, food quality, and soil physical-chemical properties was studied. For most species, warming may exert a positive effect on their abundance and population development, however, it can inhibit the survival and reproduction of hibernating species. Drought leads to low soil porosity and water holding capacity, which reduces soil fauna population and changes their community composition. Drought also can reduce the coverage of flora and alter microclimate of the soil surface, which in turn indirectly reduces fauna abundance. Climate warming and elevated atmospheric carbon dioxide can reduce litter quality, which will force soil fauna to change their dietary choices (from higher-quality foods to poor quality foods) and reduce reproduction for survival. However, it is still predicted that enhanced species richness of plant (or litter) mixtures will positively affect soil fauna diversity. Habitat loss caused by the deterioration of soil physical-chemical property is primary factor affecting soil fauna. We mainly discuss the threats of increased salinity (a major factor in arid land) to soil fauna and their potential responses to anthropogenic disturbance in saline soils. The increase in soil salinity can override other factors that favour habitat specialists, leading to negative effects on soil fauna. Moreover, we find that more studies are needed to explore the responses of soil fauna in saline soils to human activities. And the relationship of important ecological processes with soil fauna density, community structure, and diversity needs to be redefined.

Keywords: biodiversity; habitat; soil fauna; species distribution; stress factors

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1 Introduction

Soil biodiversity lies in the foundational core of the international agendas, for example, Global Soil Biodiversity Initiative (GSBI) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and in the United Nations Sustainable Development Goals (Briones, 2018). Soil faunas account for approximately one-fourth of the biodiversity on Earth and approximately three-fourths of all multicellular organisms (Coleman et

*Corresponding authors: TIAN Changyan (E-mail: tianchy@ms.xjb.ac.cn); ZHAO Shuai (E-mail: zhaoshuai@ms.xjb.ac.cn)
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al., 1996; Hoogen et al., 2019; Josef and Jose, 2021). Yet, belowground organisms have received little attention compared with aboveground organisms (Decaëns et al., 2006; Fig. 1). Soil fauna can be found in almost every terrestrial environment on Earth, including deserts, tundra, saline soils, and Antarctica (Fierer et al., 2009). Distribution patterns of soil fauna are influenced by climatic conditions, vegetation cover, and soil texture, but microbial communities are more influenced by local factors such as land use and soil type rather than by geomorphology and climate (Ranjard et al., 2010; Lavelle et al., 2022). Generally, researchers separate soil fauna into three classes based on body width (Fig. 2). Microfaunas (protozoa, nematodes, rotifers, and tardigrades) range from 2 to 100 μm in body width and inhabit soil water films. Mesofaunas range

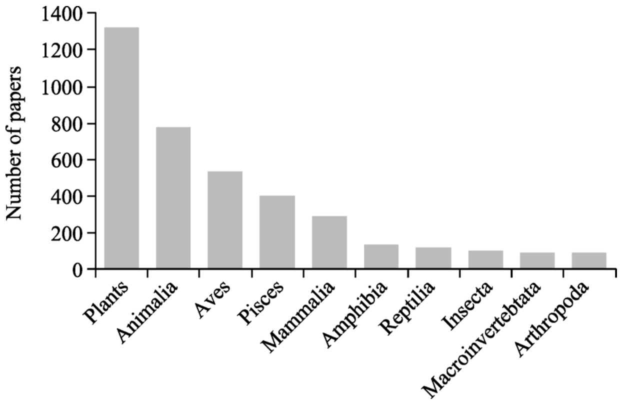

Fig. 1 Number of papers published in Web of Science on biodiversity conservation in 2021

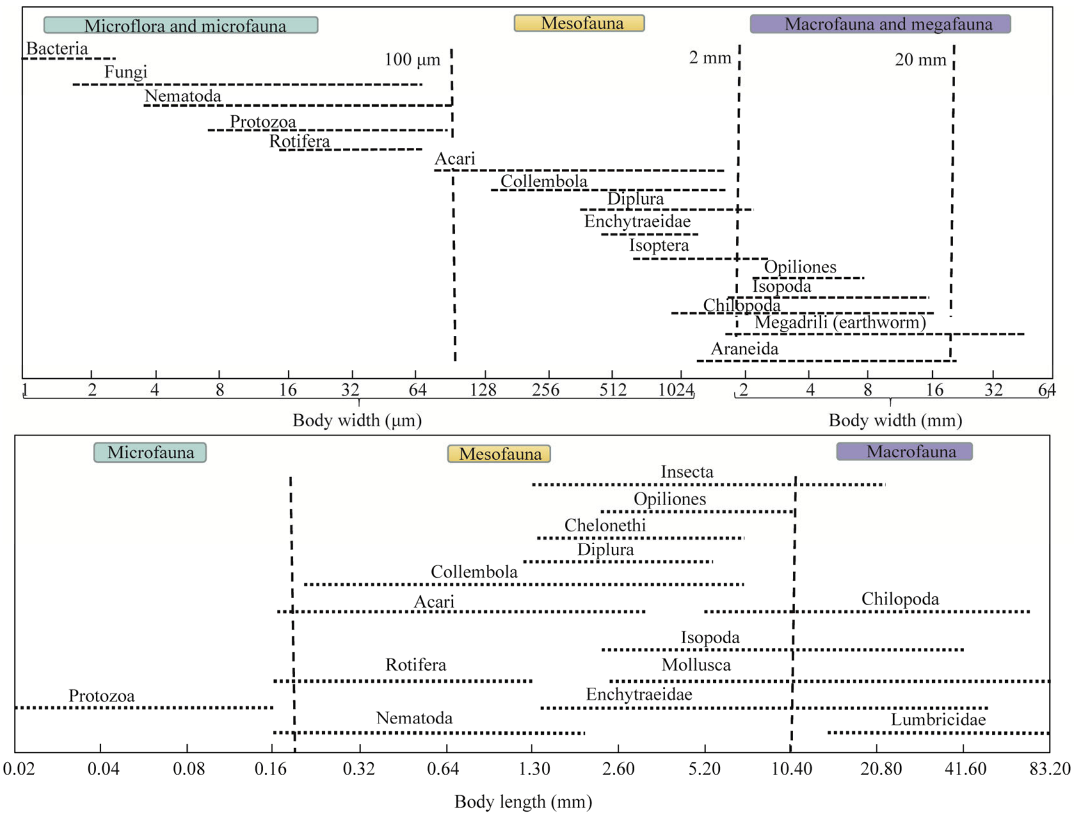

Fig. 2 Classification of soil fauna by body width and body length. On the basis of body width: microfauna (2–100 μm), mesofauna (100 μm–2 mm), and macrofauna (2–20 mm). On the basis of body length: microfauna (0.02–0.20 mm), mesofauna (0.20–10.00 mm), and macrofauna (10.00–80.00 mm).

from 100 μm to 2 mm in width and include Acari, Collembola, Diplura, and Enchytraeidae. They live in air-filled pore spaces in the soil. Macrofaunas are >2 mm wide and include earthworms and soil-dwelling vertebrates. They are able to create their own microhabitats due to their life strategy (e.g., earthworm bioturbation) (Swift et al., 1979; Lavelle and Spain, 2001).

Soil faunas play a vital role in shaping ecosystem functions, especially biogeochemical and nutrient cycling (Frouz, 2018; Joly et al., 2018, 2020). They can modulate soil nutrients by inducing the chemical binding of carbon (C) and phosphorous (P), thereby promoting the movement of organic and mineral particles (Bohlen et al., 2004; Aubert et al., 2010; Briones, 2018; Fanin et al., 2019). For example, the nitrogen (N) released from earthworm mucous, excreta, and biomass turnover is higher than that of annual litter falls in deciduous forests (Petersen and Luxton, 1982). Earthworms can also increase plant-soil N cycling by mineralizing and translocating organic matter (Blume-Werry et al., 2020). Earthworms, ants, and termites–that are referred to as ecosystem engineers–alter soil physical structure by decreasing its bulk density and increasing porosity. Such processes result in increased water infiltration, with a concomitant increase in the availability of N and other nutrients (Gong et al., 2019; Hallam and Hodson, 2020). Microarthropods and millipedes promote litter decomposition and stimulate the mobilization of various nutrients (David, 2014; Kitz et al., 2015; Garcia-Palacios, 2016; Lubbers et al., 2020). In temperate and wet tropical climates, soil faunas increased litter decomposition (Wall et al., 2008). Also, soil faunas accelerated litter mixture decomposition in dry environments (Denis et al., 2021). A global meta-analysis reported that the contribution of soil fauna to increased litter decomposition can be up to 27% (Garcia-Palacios et al., 2013). The activities of the soil fauna also affect plant productivity (Bardgett et al., 2014), e.g., the presence of protozoa stimulates N uptake by spruce seedlings (Jentschke et al., 1995) and wheat growth (Kuikman et al., 2003). Surprisingly, some studies have shown that soil fauna impact microbes and thus contribute to ecosystem functions (Nieminen, 2008; Li et al., 2021; Zahorec et al., 2021). Under nutrient-limited conditions, soil faunas do not use all immobilized nutrients to increase their biomass but supply microorganisms or plants via excretion (Ingham et al., 1985). The soil food web in deserts is composed of multiple consumers (Whitford, 1999); nematodes as consumers can influence decomposition rates by regulating activity of bacterial prey in deserts (Santos et al., 1978). Nematodes, protozoa, and their microbial food resources constitute the soil microbial food web, which influences nutrient cycling and trophic dynamics (Lavelle et al., 1997; Wardle, 2002; Yang et al., 2021). Therefore, soil fauna is crucial to maintain multiple functions of the ecosystem (Jing et al., 2015).

Soil fauna density, community structure, and diversity are susceptible to various environmental conditions (Kardol et al., 2011; Zhou et al., 2020; Yang et al., 2021). On a global scale, precipitation and temperature are the most important driving factors that affect earthworm biomass and abundance, respectively (Hoogen et al., 2019; Phillips, 2019). On regional and local scales, soil fauna diversity is affected by non-climate-related drivers, such as soil organic matter, pH, and moisture (Curry et al., 2004; Rutgers et al., 2016). For example, N-rich soils contain a greater number of bacterial-feeding nematodes (Lagerlof et al., 2002). Nematode community structure and diversity are sensitive to small fluctuations in temperature and moisture (Bakonyi et al., 2007). Pesticides are one hazard to invertebrates (Gunstone et al., 2021), and earthworms do not thrive in mining regions because of extreme soil pH, high metal content, low soil moisture, and lack of suitable food (Ronan et al., 2020). Natural events (e.g., flooding or fires) can also affect soil properties and determine the composition of soil fauna (David and Gillon, 2009; Schelfhout et al., 2017), e.g., flooding causes sharp decreases in earthworm biomass and abundance by altering soil properties (Kiss, 2019). Some newly emerging concepts, such as "biological accessibility" and "trophic cascades", are used to explain the observed faunal responses to environmental changes (Briones, 2018). All these phenomena currently affect soil fauna and are predicted to have an increasing impact in the context of global environmental changes (David and Handa, 2010; IPCC, 2014).

This review outlines recent progress in research on the responses of soil fauna to major

environmental change factors, including climate (warming and drought) and non-climate (food quality and soil physical-chemical property) factors (Fig. 3). Considering that the simultaneous occurrence of high temperature and dry climate increases soil salinity and has combined effects on soil fauna and ecosystem functioning, e.g., by modifying the quality of natural resources available to consumers (FAO, 2021), we emphasize the impact of concurrent factors on soil salinity in the soil fauna community. We then provide a holistic overview of the current knowledge regarding human activities that affect fauna in saline soils.

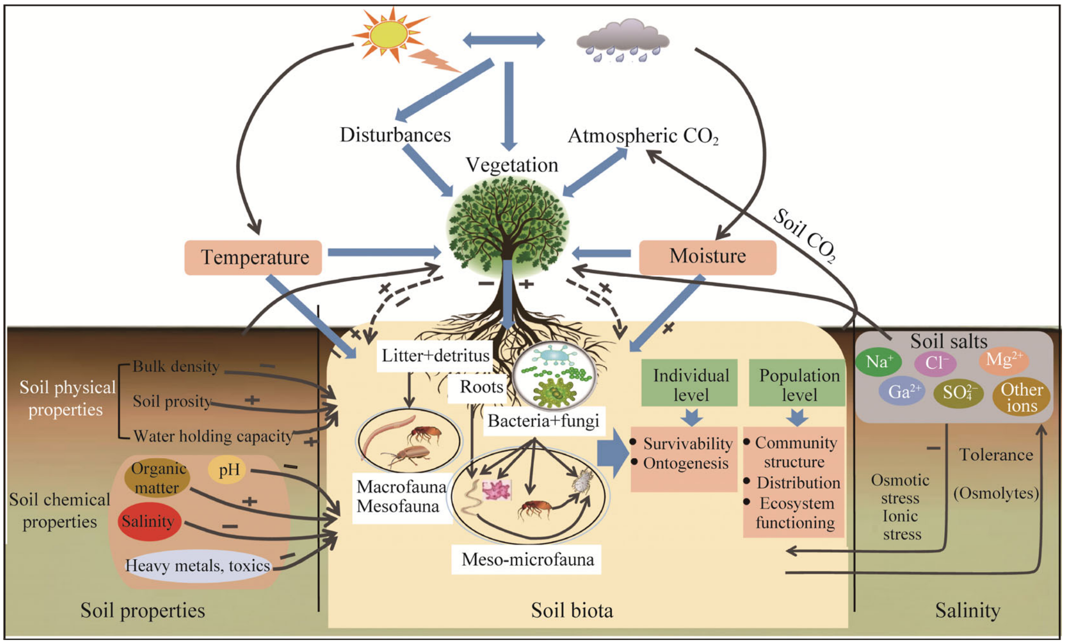

Fig. 3 Impact of key ecological factors on soil fauna and interactions of soil fauna with plants, organisms, and soil properties. Each arrow represents interaction. The solid arrows depict direct interactions, whereas the dashed arrows depict indirect effects. Plus (+) represents positive effects, and minus (–) was negative.

2 Effects of changing environmental factors on soil fauna community

2.1 Warming

Temperature affects the rate of biochemical processes in organisms. Living with higher average temperatures, species in the Southern Hemisphere have more specific adaptations to these temperature changes than those in the Northern Hemisphere (Dunn et al., 2009). Warming may have positive effects on the density and diversity of soil fauna (Table 1). For instance, warming can directly increase nematode density by promoting growth and reproduction or enhancing food supply by indirectly increasing litter input and microbial activities (Kardol et al., 2010; Mueller et al., 2016; Guo et al., 2021). A temperature increase of 3.3°C has a significant and positive effect on the polydesmid millipede, causing it to reproduce earlier in spring (David and Handa, 2010). Such positive effects of warming on population growth are common among detritus-consuming arthropods (Sinclair and Stevens, 2006), as plant cover changes associated with warming are likely to lead to changes in soil fauna communities (Thakur et al., 2014).

Yet, warming is not necessarily advantageous to population growth, particularly for macro-arthropods (Table 1; Castaneda and Aballay, 2016). For example, warming and increased carbon dioxide levels can reduce the availability of high-quality food, which negatively affects the diversity of millipedes (David and Gillon, 2009). Additionally, warming may increase the number of warm-adapted species and decrease cold-adapted species (Blankinship et al., 2011).

Table 1 Effect of warming on soil fauna community

Soil fauna community	Warming treatment		Influence	Reference
	Timing	Amount of warming		
Nematode	7 a	1.5℃ during the day; 3.0℃ during the night	Changed the community structure of nematodes. Increased the abundance of bacteria feeders and fungivores. Decreased the abundance of herbivores, predators, and omnivores.	Mueller et al. (2016)
Polydesmus angustus	300 d	3.3℃	Positive effects on abundance and higher population growth rates.	David and Handa (2010)
Microarthropods	2 a	4.0℃	The richness and diversity of microarthropods increased.	Meehan et al. (2020)
Millipedes	Four seasons	3.3℃	The diversity and growth of millipedes decreased.	David and Gillon (2009)
Microarthropods	Extreme winter warming	(0.6–3.2)℃ (soil); 3.5℃ (soil surface)	Acari populations decreased by 39%; Collembola shifted from smaller soil-dwelling (euedaphic) species to larger litter-dwelling (hemiedaphic) species.	Bokhorst et al. (2012)
Spirostreptid millipede (*Orthoporus ornatus*)	Desert warming for a season	Slight warming	High temperatures depleted the fat reserves of hibernating species, negatively affecting their growth in the following season.	Crawford et al. (1987)
Microarthropods	2 a	1.3°C	Warming had insignificant effects on the abundance of mites and Collembola.	Wu et al. (2011)
Soil fauna community	Experimental stage	(1.0–2.0)°C	Warming did not affect the density and diversity of soil fauna community.	Peng et al. (2022)

Arctic warming may lead to an increase in soil fauna diversity, but extreme winter warming decreases Acari population sizes and shifts Collembola communities from euedaphic, soil-dwelling species to larger, hemi-edaphic, and litter-dwelling species (Bokhorst et al., 2012). Evidence suggests that the impact of warming on soil fauna depends on precipitation (Lindberg et al., 2002; Blankinship et al., 2011; Landesman et al., 2011; Kardol et al., 2011; Meehan et al., 2020). A recent study showed that soil faunal diversity is resistant to global warming, whereas soil faunal density is mainly affected by rainfall (Peng et al., 2022). In arid soils, the abundance of Collembola and mites is affected by drought but not by climate warming (Wu et al., 2011). Because global warming stimulates temperature-associated drought in many areas (Yue et al., 2019), drought has become a strong force to be reckoned by soil fauna.

2.2 Drought

Under drought conditions, it is difficult for animals to move because of the increased compactness of the soil and decreased soil water film (Coleman et al., 2004). Changes in event size and frequency of precipitation influences invertebrate activity and density in dryland ecosystems (Nielsen and Ball, 2015). The effects of drought on soil fauna tend to be negative (Table 2). Many groups, including Collembola, nematodes, enchytraeids, and earthworms, are highly sensitive to soil moisture (Holmstrup et al., 2001; Wang et al., 2020). Drought has less effect on soil fauna diversity, but it can decrease soil fauna density by 27.4% (Peng et al., 2022). The reproduction and survival rates of the potworm (*Enchytraeus crypticus*), and white worm (*Enchytraeus albidus*), decline by >23% under drought conditions, particularly after prolonged exposure to drought (Maraldo et al., 2009). However, some species, such as the oribatid mite *Licnodamaeus pulcherrimus* and *Pseudosinella alba*, adapt well to drought (Guidi et al., 2002). The range and abundance of Argentine ants (*Iridomyrmex humilis*) decrease in dry soil, whereas the population density of fungus-gardening ants (drought-resistant species) increases during periods of drought (Seal and Tschinkel, 2010). Almost all functional groups of nematodes are sensitive to drought, but Qudsianematidae species do not appear to be significantly affected (Williams and Jackson,

2007). Holmstrup et al. (2007, 2017) found that springtails could recover from recurring drought events. This is because springtails have survival strategies that include moving to moist microsites, assuming an anhydrobiotic state, and resisting drought by reducing the permeability of their integument (Greenslade, 1981; Liu et al., 2021).

Drought also indirectly affects soil fauna community (Franklin et al., 2016), e.g., causing a shift in species distribution. Drying conditions in southwestern Australia have caused moisture-favouring millipedes (e.g., Sphaerotheriida and Polyzoniida) to be outcompeted by drought-tolerant species (e.g., *Antichiropus* sp.), thus creating new species boundaries (Moir et al., 2009). Drought is also correlated with food availability and thus influences soil fauna. Low water availability reduces the activity of microorganisms and leads to a decrease in faunal populations (Peguero et al., 2021). The abundance of collembolans and oribatid mites decreased by 80.6% and 77.8%, respectively, at a drought area because only 40% of the litterfall occurred during the drought treatment (Lindberg et al., 2002).

Table 2 Effect of drought on soil fauna community

Soil fauna	Drought treatment	Influence	Reference
Enchytraeus crypticus and *Enchytraeus albidus*	4 d exposed to a decreasing relative humidity from 99.8% to 98.4% 99.8% relative humidity (–2.7 Pa) 98.4% relative humidity (–22.1 Pa)	Reproduction and survival of *Enchytraeus crypticus* and *Enchytraeus albidus* declined >23% under drought conditions.	Maraldo et al. (2009)
Soil dwelling springtail	28 d exposed to a water potential from 0 to –85 kPa (with an accuracy of ±20 kPa)	Reproduction stopped at soil water potentials (–15 kPa), which did not influence body water content or growth. Body growth and activities continued until −100 kPa.	Wang et al. (2020)
Earthworm (*Aporrectodea Caliginosa*)	Drought exposure 14 d between –2 and –300 kPa	Cocoon production was arrested when water potential was lower than –12 kPa and below –40 kPa. Under severe drought levels (–330 kPa), cocoon production was significantly impaired 2 months after drought exposure.	Holmstrup et al. (2001)
Soil fauna community	Extracted drought data from the WorldClim database	Soil fauna density was reduced by 27.4% under the drought condition.	Peng et al. (2022)
Soil fauna community	Preventing 70% of the throughfall on the plots from reaching the ground from April to September	The Oribatida abundance decreased by 77.8% in the drought treatment. Collembola abundance was reduced by 80.6%. Enchytraeids, mesostigmatid mites, and macroarthropod predator density decreased.	Lindberg et al. (2002)
Soil fauna community	Dry control: 15% (±1%) water content from May to July	Acari and Collembola community composition shifted, with a higher presence of drought-sensitive species in irrigated soils.	Guidi et al. (2002)
Fungus-gardening ant	Dry treatment for 3 a, April to June every year	Fungus-gardening ants (drought-resistant species) increased in abundance during multiyear droughts.	Seal and Tschinkel (2010)

2.3 Food quality

Feeding habit is critical to the health of individuals and populations, as well as basic driver of food web structure (Ho et al., 2019). Macro-arthropods have a diverse diet (Steinwandter and Seeber, 2020) and prefer litter mixtures to single litters (De Oliveira et al., 2010). Microarthropods are omnivorous and feed on decaying plants, nematodes, bacteria, fungi, algae, and other collembolans (Eisenbeis and Wichard, 1987). As an important food resource for collembolans, the fungal growth rate and morphology have been found to change in response to predation (*Folsomia candida*) (Wood et al., 2006). The composition and function of soil microorganisms may also affect the growth and propagation of Collembola, resulting in abundance changes that affect grazing intensity (Tordoff et al., 2008). However, the feeding preference of Collembola is more affected by litter type than by fungi, whereas their reproduction is affected by both fungal species and litter type (Hedĕnec et al., 2013).

Researchers divided nematodes into five trophic groups according to their feeding habits: bacteria feeders, fungivores, predators (feeding on other nematodes), omnivores (feeding on

protozoa, bacteria, algae, fungi, and plant roots), and herbivores (feeding on plant roots) (Yang et al., 2020). Nematodes choose food and adjust their diet to maintain a balance between reproduction and survival (Laskowski et al., 2020). For example, *Caenorhabditis elegans* produced more offspring after consuming its preferred bacterial species, but reduced brood size when the preferred food was limited (Mukhopadhyay and Tissenbaum, 2007; Yu et al., 2015). *Acrobeloides* sp. feeding on their preferred soil-dwelling bacterial species had the largest brood size and a moderate survival time. By comparison, *Acrobeloides* sp. produced the smallest brood size and had the shortest survival time when they consumed their least-preferred bacterial species (Liu et al., 2017). Plants, soil properties, and climate influence soil microbiomes (Fierer et al., 2009; Joly et al., 2018, 2020; Fanin et al., 2019), and thus can indirectly affect bacterivores and fungivores. A study found ash only formed arbuscular mycorrhiza but lacked ectomycorrhizal fungi, which benefited bacterial-feeding nematodes, but suppressed fungal feeders. By contrast, beech beneficially affected fungal feeders by increasing fungi (Cesarz et al., 2013). However, if nematodes are exposed to a stressful environment (parasites, predators, and toxins), they can switch their dietary choices from higher-quality foods to poor-quality foods (Zhang et al., 2005). Amoebae and phagocytic protists can feed on fungi, bacteria, and nematodes, whereas some probiotic protists primarily feed on decomposing plant material (Geisen et al., 2016).

Plant diversity and composition may have a significant correlation with soil fauna (Frouz, 2018; Peng et al., 2020). High litter quality with high N, low phenolics, low lignin, and structural carbohydrates support bacterial-based energy channels (fast nutrient turnover), which may affect bacterial-feeding animals (e.g., dipteran larvae); in contrast, low-quality litter may affect fungal feeding animals (e.g., Collembola and mites), while maintaining a high density of enchytraeid worms and macro-microarthropods (Wardle et al., 2004). Increased aboveground productivity may support a greater abundance of soil fauna owing to higher root biomass (Ma and Chen, 2016), litter content (Saetre and Baath, 2000; Zheng et al., 2019), and microbial community diversity (Bardgett et al., 1999; Chen et al., 2019). However, few secondary compounds in some litter types can be detrimental to microbial decomposers and detritivorous consumers (Gessner et al., 2010).

Experimental plots with rich plant diversity were also found to maintain greater soil fauna abundance and diversity than that with plant monocultures (David and Handa, 2010). Multiple resources in litter mixtures can increase microhabitat complexity and food diversity (Gessner et al., 2010), which significantly supports higher soil faunal diversity (Wardle, 2006). Climate warming and elevated atmospheric carbon dioxide can alter the composition of plant communities and thus reduce litter quality; however, negative impacts on macroarthropod diversity are unlikely to counteract the positive effects of warming on population growth rates (David and Handa, 2010). Therefore, it is predicted that the diversity of soil fauna increases with the species richness of plant (or litter) mixtures. Nutrients are scarce and/or supply is discontinuous in extreme environments (i.e., cold and arid ecosystems), thus resulting in low soil biodiversity and shortage of food chains. Any nutritional surplus leads to a "hot moment" under these conditions (Kuzyakov and Blagodatskaya, 2015). Extreme events (e.g., extreme hot, cold, or precipitation) occurring frequently could affect food quality, and thereby will "cascade" along the soil food web bringing other pressures (e.g., predation and competition), which will influence soil fauna.

2.4 Habitat

Soil nutrient availability is often positively correlated with soil fauna community abundance and diversity (Zhang et al., 2014; Zhang et al., 2017). An increase in soil organic matter content provides more food resources for soil fauna which, in turn, increases their abundance and diversity (Yin et al., 2018). Group numbers and abundance of soil fauna increase with increasing soil water content, whereas higher soil temperatures result in lower soil fauna diversity (Coulibaly et al., 2022). Soil pH also affects soil fauna community. For example, pH is negatively correlated with soil fauna density in weakly alkaline soils (pH ranging from 7.52 to 8.96), whereas it is positively correlated with soil fauna density in acidic soils (pH ranging from 5.21 to 5.72) (Liu et al., 2021). A study showed that pH can affect soil food web composition, indirectly affecting nematode

community structure (Matute et al., 2013; Yang et al., 2022). Low pH and high soil inorganic N may lead to soil fauna diversity having a negative correlation with aboveground biodiversity (Wu et al., 2011). However, the mechanism by which pH directly affects soil organism remains unclear.

The primary factor affecting the extinction of soil fauna is habitat loss caused by the deterioration of soil physical-chemical property (Veresoglou et al., 2015). For example, urbanization fragments the soil surface, leading to the elimination of autotrophic organisms and a subsequent reduction in macrofaunal biomass (Pavao-Zuckerman and Coleman, 2007). Soil tillage can negatively affect soil fauna by destroying soil aggregates (Rillig and Mummey, 2006). Increases in atmospheric carbon dioxide concentrations indirectly lead to decreases in soil aggregation and pore size, which may cause the elimination of some soil fauna species (e.g., Collembola) living in pore spaces (Niklaus et al., 2003). Soil contamination alters the predator/prey ratio in the soil (Edwards, 2002). For example, the survival of enchytraeids and earthworms declines in the soil containing petroleum, and the abundance of isopods in contaminated areas is higher than that in uncontaminated areas (Faulkner and Lochmiller, 2000). Habitat loss caused by chemical stressors (e.g., soil pollution) can lead to the loss of the most sensitive species and promote the tolerance of invasive or opportunistic species (Syrek et al., 2006; Piola and Johnston, 2008; Beaumelle et al., 2021).

Soil salinity significantly affects the distribution of soil organisms (Placella et al., 2012). Saline soils (>800×10^6 hm^2) represent 6% of the world's total land area (FAO, 2008) and harbor a large number of soil animals (Andronov et al., 2012). Yin et al. (2018) reported that Prostigmata, Oribatida, Gamasina, Collembola, Entomobryidae, and Isotomidae are the dominant groups in the salinized soils of Songnen Grasslands, China. By comparison, enchytraeids and the majority of arthropods, except for collembolans, are more abundant in the salinization sites in Northwest England (Kevin and Butt Maria, 2017). Increases in salinity affect the distribution of soil animals. Therefore, the following section of this paper focuses on the relationship between salinity and soil fauna, and discusses the responses of soil fauna to increasing salinity.

2.4.1 Responses of soil fauna to soil salinity

Soil salinity is a hazardous factor for soil fauna (Table 3). High salinity poses a direct physiological challenge to soil fauna, primarily via osmotic and ionic stress (Price et al., 2004). Ionic stress causes the death in protozoa by cytoplasmic membrane rupture and cell death (Li et al., 2017). Nematodes cannot survive in high-saline soils at 4100 μS/cm (Nkem et al., 2006). Salinity causes a sharp decline in soil nematode abundance (on average 1/100 mL of soil) compared with non-salinized areas (on average 25/100 mL of soil) (De et al., 2020). Earthworms can grow only at salinity levels ≤5436 mg/kg NaCl and breed only when salinity is below 4985 mg/kg NaCl (Owojori et al., 2008). Soil salinity increases Pb (lead) toxicity and significantly decreases earthworm activity (Raiesi et al., 2020). In addition, salinity decreases the litter decomposition rate (Roache et al., 2006; Zhai et al., 2020), which indirectly affects the number of soil fauna detritivores that rely on decomposing plant litter as a food resource (De et al., 2021; Venâncio et al., 2021). Salinity stress is also associated with drought and warming, for example, high salt concentration is expected in soils as a result of sea level rise and warming (Bindoff et al., 2019), which leads to the decline in hydraulic conductivity, water infiltration, organic matter solubility, and soil porosity (Wong et al., 2010; Amini et al., 2016). Such environment deterioration can aggravate the detrimental effects of salinity on organisms (Wang et al., 2001; Kristin and Johannes, 2015).

The basic behavioural response of soil fauna to detrimental increases in soil salt is to move. To avoid high-salinity environments, the collembolan *Cryptopygus antarcticus* migrates to more suitable microhabitats (Elnitsky et al., 2008). Earthworms have clear avoidance responses to higher soil salinity (Owojori et al., 2009; Owojori et al., 2014). In avoidance tests, *Aporrectodea caliginosa* was a sensitive species, regardless of the soil properties or ionic composition. Physiological adaptations, such as a continuous exoskeleton, can reduce contact between an organism and soil salt (O'Connor, 2003; Pereira et al., 2015). Due to their impermeable membranes, *Heterochaeta costata* and *Enchytraeus albidus* (annelids) can survive in saline soils

Table 3 Effects of salinity on the soil fauna community

Soil fauna	Salinity treatment	Influence	Response	Reference
Protozoa	$NaHCO_3$, NaCl, $KHCO_3$, and KCl at 160 mM	Ionic stress led to cell death of protozoa. $NaHCO_3$ was shown to be the most effective inhibitor.	Although protozoa do not contain a rigid cell wall, they can develop osmoregulatory mechanisms to minimize the damage caused by hyper-osmotic conditions.	Li et al. (2017)
Nematode *Scottnema lindsayae* and *Plectus antarcticus*	NaCl, $MgSO_4$, KNO_3 and NaCl+$MgSO_4$, concentrations ranging from 0.1–3.0 M	Salinity reduced the survival of both nematode species.	Species have different salt tolerance. *S. lindsayae* survived in <0.2 M NaCl and <0.5 M $MgSO_4$. They did not survive in any concentration of NaCl+$MgSO_4$. *P. antarcticus* survived in <0.5 M NaCl, <0.5 M $MgSO_4$, and <0.2 M (NaCl+$MgSO_4$).	Nkem et al. (2006)
Earthworm	NaCl concentrations: 0, 1000, 2000, 4000, 6000, and 8000 mg/kg	The survival, growth, and cocoon production were limited above the concentrations of 5436, 4985, and 2020 mg/kg NaCl.	Behavioural strategy: earthworms escaped a high salinity environment. The avoidance of *A. caliginosa* of 667 mg/kg NaCl. The avoidance of *E. feida* of 1164 mg/kg NaCl.	Owojori et al. (2009); Owojori et al. (2008)
Spider (*Arctosa fulvolineata*)	Three concentrations of substrate salinity (0‰, 35‰, and 70‰)	Survival and egg-laying were significantly impaired when exposed to hypersaline conditions for 12 d.	Morphological adaptations: having a continuous exoskeleton reduced body contact with salt. Physiological adaptation: accumulation of osmo-induced amino acids increased the osmolality of body fluids, enhancing the survival ability of spiders.	O'Connor (2003); Foucreau et al. (2012)
Nematode	Salinized Caatinga EC: 65.6, 106.2 dS/m; Natural Caatinga EC: 0.98, 1.30 dS/m	Salinity caused a sharp decline in nematode abundance.	Nematodes employed anhydrobiosis (reduced metabolic activity) to survive in dry and salty conditions.	Zhi et al. (2008)
Soil fauna community	Salinization habitat: 0.19%, 0.26%, 0.47%, 0.68%, and 1.12%.	High salinity decreased the number of taxa. Community composition changed significantly.	Different soil fauna taxa exhibited various tolerance to salinity.	Yin et al. (2018)
Decomposer fauna	Water salinity treatment: 10.0%, 5.0%, 3.0%, 1.0%, and 0.4%	High salinity (>5%) decreased the litter decomposition rate. Modest salinity increased the litter decomposition rate	Plots with 3% salinity showed higher decomposition rates than plots with 1.0% salinity and 0.4% salinity.	Zhai et al. (2020)

Note: EC, electrical conductivity.

(Generlich and Giere, 1996). Osmoregulatory organs, such as coxal glands and sclerotized rings in the cuticle, have been reported in mites (Bayartogtokh and Chatterjee, 2010).

Some species adjust their metabolic states to cope with environmental stressors. For example, nematodes employ anhydrobiosis (reduced metabolic activity) to survive in the dry and saline Negev Desert (Zhi et al., 2008). Fungivorous nematodes (*Aphelenchoides*, *Ditylenchus*, and *Filenchus*) and bacterivorous nematodes (*Chronogaster* and *Rhabdolaimus*) dominate in salt-affected alluvial soils (Nguyen et al., 2021). *Caenorhabditis elegans* avoids salt when faced with an absence of food, but is attracted to salt after exposure to food (Adachi et al., 2010). The beetle *Merizodus* and spider *Arctosa fulvolineata* increase the osmotic pressure of their body fluids by accumulating amino acids (Foucreau et al., 2012). Some terrestrial arthropods can survive in soils with up to 70% salinity (Pétillon et al., 2011) because they accumulate substances that contribute to osmoregulation, including disaccharides, monosaccharides, and quaternary amino acids (Misra and Misra, 2012).

2.4.2 Human activities to remediate soil salinity are changing the fauna community

Human activity-induced salinity (generally referred to as secondary salinization), in combination with climate change, leads to greater harm than salinity alone (Yeo, 1998). We have applied many strategies to cope with increased salinity, including the extensive use of fertilizers (Zheng et al., 2019) and biologically treating saline soils (Wang et al., 2020). The responses of soil fauna

organisms to fertilization vary greatly, depending on the type of fertilizer used. Higher carbon and N ratios promote the increases in fungal activity and biomass, providing more food for fungivorous nematodes (Deng et al., 2016). Long-term application of organic manure increases the diversity of predatory soil fauna and earthworms in grassland soils (López-Hernandez et al., 2004). The abundance, community composition, structure, and diversity of soil fauna increase after the addition of organic fertilizer to saline soil (Banerjee et al., 2009). N application significantly reduces the number of soil nematodes and protozoa (Qi et al., 2011). N fertilization can be increased with the degree of salinization to improve aboveground crop biomass in saline soils—this led to a 50% increase in fertilizer use in heavily salinized fields in China (Zheng et al., 2019). As aboveground productivity has positive effects on soil fauna, the question is whether such effects can be offset by the negative influence of N fertilizers.

Halophytes are salt-tolerant plants and their culture is often employed to reclaim saline soils. Planting halophytes would affect soil fauna due to the following reasons: (1) halophytes reduce soil salinity by absorbing salt from soils, and lower salt stress may promote the growth of soil fauna. Also, lower salt stress led to an increase in soil microbiome populations (Wang et al., 2020), which may be beneficial to predators that prey on microorganisms; (2) habitat heterogeneity is favourable for microarthropod diversity (Tews et al., 2004; Samways, 2007). A study found that the abundance of millipedes in nature reserves depends more on land cover heterogeneity than the size of the reserve (Sadler, 2008). Therefore, cropping halophytes would trigger habitat heterogeneity in saline soils, which may positively affect soil fauna; and (3) small differences in litter quality and quantity in forest ecosystems are determinants of arthropod diversity (Sayer et al., 2010). In European subalpine spruce forests, the abundance of springtails is higher in young forests, whereas that of Oribatida is higher in mature forests with high litter input (Salmon et al., 2006). Halophyte litter may increase resources (e.g., organic matter and proteins) that are beneficial to consumer organisms. Moreover, plants are not merely suppliers of litter or habitat for soil fauna—they produce secondary metabolites that attract beneficial soil invertebrates, such as entomopathogenic nematodes to kill herbivores (Bonkowski et al., 2009). Halophytes might directly affect belowground communication through rhizospheres and this warrants further study.

2.4.3 Research implications for fauna communities under soil salinity

Saline areas are experiencing a general increase. This is predicted to intensify in the future due to climate change. Soil biodiversity plays an essential role in regulating ecosystem services (Wagg et al., 2014; Delgado-Baquerizo et al., 2020; Fan et al., 2021). Therefore, increases in salinity will have an impact on the structure and functioning of ecosystem by affecting soil fauna. A better understanding of soil fauna in saline soils is essential not only to conserve biodiversity, but also to ensure the maintenance of key ecosystem services in the face of climate change, particularly in the context of the FAO's proposed "halt soil salinization, boost soil productivity" (FAO, 2021). Studies can focus on two aspects: (1) establish a monitoring system for soil ecosystems using soil fauna communities (e.g., biodiversity or components) as indicators of specific ecosystem functions, as they are linked to fauna adaptation strategies in response to climate, soil resources, disturbances (e.g., land-use change), and defence/protection needs; and (2) develop methods to predict future changes in soil fauna communities and soil faunal-driven ecosystem processes. Interactions between environmental factors, such as N deposition, carbon dioxide enrichment, the frequency of extreme events, and increased human pressure, can have cumulative joint effects on soil fauna communities (David and Handa, 2010). Additionally, the ecological consequences of biotic interactions (e.g., microorganism, disease, parasitism, and predation) can affect the abundance and distribution of soil fauna. Therefore, building bridges between disciplines and bringing together available information, e.g., molecular biological information (environmental DNA (deoxyribonucleic acid) and various 'omics' approaches), activity proxies, acoustic signatures, and response traits, will allow a more realistic assessment of their response to environmental change.

3 Conclusions

This review addressed the key environmental factors affecting soil fauna and the potential risk posed to fauna communities by changing climate. Warming may have a positive impact on the abundance and development of most species, but will inhibit the survival and reproduction of hibernating species. Drought reduces soil fauna populations in many areas and alters their community composition. The reduced food quality will make soil fauna change their dietary choices (from higher-quality foods to poor quality foods) to reduce the reproduction for survival. However, enhanced floral diversity will still contribute positively to the diversity of soil fauna. Any loss in habitat caused by deterioration of soil physical-chemical property may be directly detrimental to soil fauna. It should be noted that an increase in soil salinity could override other factors that favour habitat specialists, leading to negative effects on soil fauna. The response of soil fauna to environmental factors in saline soils requires further study. This information may help to guide preventive strategies (e.g., biodiversity conservation) and/or corrective measures (e.g., inclusion of specific species in restoration projects) to protect the threatened ecosystem.

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